THE BIOLOGY AND FUNCTIONAL MORPHOLOGY OF THE TWISTED ARK
TRISIDOS SEMITORTA (BIVALVIA: ARCACEA)
WITH A DISCUSSION ON SHELL "TORSION" IN THE GENUS

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ABSTRACT

The biology and functional morphology of the twisted ark *Trisidos semitorta* (Lamarck) are described. The adult occupies clean sands, with the anterior end buried and the anterior sagittal plane vertical to the surface. Because of posterior shell twisting, the posterior face of the right valve lies beneath that of the left which projects above the sand surface. The posterior sagittal plane of the shell thus lies parallel with the sand-water interface. The mode of life of the juvenile is also described for the first time. It lies within the inner surface of empty bivalve shells, firmly attached by a byssus. Juveniles of both *T. semitorta* and *T. tortuosa* (Linnaeus) are less twisted than adults, the two species being similar when young. The adult *Trisidos* can be derived from an ancestor in which anatomical modifications adapting it to a byssally attached, nestling mode of life have been retained, indeed enhanced, in the transition from juvenile to adult to permit colonization of sands with fast-flowing currents above. Only the posterior region of the shell is twisted about the dorsoventral axis of ligament and byssus. In the free-living adult the byssus is absent, but the growth processes begun in the juvenile are continued into adult life. Shell twisting results from the contraction of asymmetrically developed posterior pedal retractor muscles, the left being larger and lying behind the diminutive right. This is analogous to the phenomenon of torsion in the Gastropoda, but the end result is different and the term twisting, and not torsion as used by McGhee (1978), more aptly defines the process of *Trisidos*.

Key words: *Trisidos*; anatomy; twisting; posterior pedal retractors; evolution.

INTRODUCTION

Members of the arcid genus *Trisidos* are unusual in being twisted. More particularly, it would seem as though the anterior end of the shell had been held stable and the posterior end twisted through approximately 90°. This phenomenon has been studied most recently by McGhee (1978) and Tevesz & Carter (1979) in species, e.g. *T. tortuosa,* in which twisting is most obvious. The first study is a largely theoretical account of the pattern of torsion (the term being used synonymously with twisting by the former author) within the Arcidae and extinct Bakevelliidae. The latter account derives *Trisidos* from a *Barbatia*-like ancestor but is of insufficient detail to confirm or deny this hypothesis. The anatomical description is superficial.

Most authors describe twisting in *Trisidos*, but neither demonstrates *how* it occurs in this unusual group of animals. An understanding of *Trisidos* may cast light on the mechanism of twisting in the Bakevelliidae, the only other group of twisted bivalves (McGhee, 1978).

Little is known of the biology of *Trisidos*.

The adult is known to inhabit soft deposits into which it can reburrow, but the mode of life of the juvenile is unknown.

This study was initiated when juveniles of *T. semitorta* were found. Juvenile adaptations cast light on how shell twisting in the adult is achieved and the claim by Tevesz & Carter (1979) that the *Trisidos* ancestor was a *Barbatia*-like nestler.

MATERIALS AND METHODS

Adult and juvenile specimens of *Trisidos semitorta* were obtained with an Agassiz trawl from about 8 m of water in the NE territorial waters of Hong Kong (Mirs Bay), some 3 km to the ESE of the village of Sha Tau in the People's Republic of China (grid reference 225,994 from 1:100,000.L681, 1970).

The sea bed comprises a coarse sand and is covered by empty shells (occupied by the juvenile *T. semitorta*) of the bivalves *Anadara antiquata* (Linnaeus) and *Tapes dorsatus* (Lamarck). Also present is the burrowing ark *Cucullaea concamerata* (Martini) (Morton,

1981) and the shell boring gastrochaenid *Cucurbitula cymbium* (Spengler) (Morton, 1982). The samples were hosed down in a 5 mm sieve and returned to the departmental sea water aquarium. Large specimens were separately placed in shallow tanks with a thick bed of sand and circulating sea water.

The ciliary currents of the organs of the mantle cavity and the stomach were elucidated using carmine in sea water. Two small specimens were fixed in Bouin's fluid and serially sectioned at 6 μm. The sections were stained in either Ehrlich's haematoxylin and eosin or Mallory's triple stain.

Specimens of *Trisidos tortuosa* in the collections of the British Museum (Natural History) have been examined as follows:

11 adult (dried valves) (BM (N.H.) reg. no. 1953.1.23.377) from Singapore. R. Winckworth collection. Acc. No. 1838.
6 juveniles (dried valves) (no reg. no.) from Karachi, India. F. W. Townsend collection. Acc. No. 1831.
1 adult (alcohol preserved) (Reg. no. 81.11010) from Port Collis. 11 fathoms 'Alert' collection.

The latter specimen was opened to confirm details of the posterior pedal retractor muscles previously noted for *T. semitorta*.

ABBREVIATIONS USED IN THE FIGURES

A	A cell layer of the style sac
AA	anterior adductor muscle or scar
AA(Q)	"Quick" component of the anterior adductor muscle
AA(S)	"Slow" component of the anterior adductor muscle
AN	anus
AP	anal papilla
APP	anterior pedal protractor muscle
APR	anterior pedal retractor muscle
ASO	abdominal sense organ
AU	auricle
B	B cell layer of the style sac (the major typhlosole)
B_1	B_1 cell layer of the stye sac (the minor typhlosole)
BG	byssal gland
BY	byssus
BYG	byssal groove
C	C cell layer of the style sac
CA	ctenidial axis
CFC	coarse frontal cilia
CR	"chitinous" rod
CS	crystalline style
CSM	conjoined style sac and mid-gut
CSS	crystalline style sac
D	D cell layer of the style sac
DD	digestive diverticula
DDD	duct to digestive diverticula
DH	dorsal hood
EA	exhalant aperture
F	foot
FC	food sorting caecum
FFC	fine frontal cilia
FGC	filament gland cell
FO	fold in the stomach wall
FS	fragmentation spherules
G	gonad
GO	gonoduct
GP	gonopore
GS	gastric shield
H	heart
HG	hind-gut
IA	inhalant aperture
ID	inner demibranch
IG	intestinal groove
ILP	inner labial palp
IME	inner mantle epithelium
IMF	inner mantle fold
K	kidney
LC	lateral cilia
LEC	left ctenidium
LFC	latero-frontal cilia
LP	left pouch
MG	mid-gut
MI	mantle isthmus
MMF	middle mantle fold
MT	minor typhlosole
N	nerve
NF	nerve fibers
NU	nucleus
O	oesophagus
OC	*Oulastrea crispata*
OD	outer demibranch
OFM	oblique fibres of mantle
OLP	outer labial palp
OME	outer mantle epithelium
OMF	outer mantle fold
P	periostracum
PA	posterior adductor muscle or scar
PA(Q)	"quick" component of the posterior adductor muscle
PA(S)	"Slow" component of the posterior adductor muscle
PE	pericardium
PEG	pedal gland
PG	pallial glands
PO	*Polydora* sp.
PPR(L)	left posterior pedal retractor muscle
PPR(R)	right posterior pedal retractor muscle

PRM   pallial retractor muscle
R   ridge entering the dorsal hood
RA   renal aperture
RE   rectum
RPA   reno-pericardial aperture
SA   sorting area of the stomach
SC   secretory cell
SEC   sensory cell nucleus
T   major typhlosole
TF   transverse fibres
TFM   transverse fibres of mantle
V   ventricle

TAXONOMY

Trisidos Röding, 1798 is a genus of the family Arcidae (see Newell, 1969 for taxonomic details), the latter being divided into two subfamilies—the Arcinae Lamarck, 1809 and the Anadarinae Reinhart, 1935. The former are generally considered to be either powerfully attached nestlers, e.g. *Barbatia* Gray, 1842 and *Arca* Linnaeus, 1758, or borers, e.g. *Litharca* Gray, 1842, while the latter are typically either burrowing and abyssate, e.g. *Anadara* Gray, 1847, *Scapharca* Gray, 1847 or but weakly byssally attached, e.g. *Bathyarca* Kobelt, 1891 and *Bentharca* Verrill & Bush, 1898. Despite this disparity in habitat, Newell (1969) places the burrowing, abyssate *Trisidos* in the Arcinae—a suggestion that will be discussed here.

The genus *Trisidos* is relatively modern (Eocene) and has an Indo-Pacific distribution. The type-species is *T. semitorta* Lamarck, 1819. According to Oyama (1974), there are three other species of the genus: *T. torta* (Mörch), *T. kiyonoi* (Makiyama) and *T. tortuosa* (Linnaeus). Oyama considers *T. yongei* Iredale to be a junior synonym of *T. tortuosa*. The form of *Trisidos* is very variable and some of these species may be in doubt, the genus warranting careful taxonomic revision.

BIOLOGY

Juvenile specimens of *Trisidos semitorta* are byssally attached and in Hong Kong waters occupy the inner surfaces of empty, large bivalve shells (Fig. 1). The byssus is relatively large and the animal is securely attached. It has been recorded from *Tapes dorsatus, Anadara antiquata* and adults of its own species. This habit undoubtedly ensures protection both from predators and from the rapid water movement that must occur over the well-aerated sands the adult inhabits. As the bivalve grows, the host shell must become more restrictive until a time is reached when the juvenile detaches. At this time the byssus is lost and the adult assumes a burrowing mode of life. *Cucullaea concamerata* occurs in the same habitat and is also adapted for fast current speeds (Morton, 1981). Observations on adult *T. semitorta* have shown that, as with *T. yongei* (Tevesz & Carter, 1979), reburrowing can occur though this process is slow, taking many days to complete.

Typically, the shell of *T. semitorta* is eroded posteriorly and colonized by other organisms, mostly on the left valve (Figs. 2, 3A). Colonizing species include the scleractinian coral *Oulastrea crispata,* the boring polychaete worm *Polydora* sp. and small *Lithophaga malaccana* (Reeve). Thus, the often extensively damaged posterior surface of the left valve projects above the sand surface while the remainder of the shell is buried. Makiyama (1931) has figured *Arca* (= *Trisidos*) *kiyonoi* in its natural position in the sand.

In Hong Kong occasional adult specimens of *T. semitorta* have been collected intertidally from sand flats in Hoi Sing Wan (Starfish Bay), Tolo Harbour and more frequently by Agassiz trawl off this and other beaches.

Tevesz & Carter (1979) report a similar habitat for *T. yongei,* i.e. a muddy, fine to medium sand subject to the effects of tidal currents and wave action and containing abundant fragmental shell material.

FUNCTIONAL MORPHOLOGY

The shell

The aragonitic shell of *Trisidos tortuosa,* as in other members of the Arcacea (Taylor, Kennedy & Hall, 1969), comprises a crossed lamellar outer layer and a complex crossed lamellar inner layer though, unusually, the pallial myostraca is prismatic in the umbonal regions only.

Both *T. semitorta* and *T. tortuosa* are antero-posteriorly elongate, with a long multivincular ligament. The hinge plate is narrow with a continuous row of taxodont teeth. These are represented only by minute projections under the central part of the hinge. Laterally, however, the teeth are relatively large and function in valve alignment and in preventing shear.
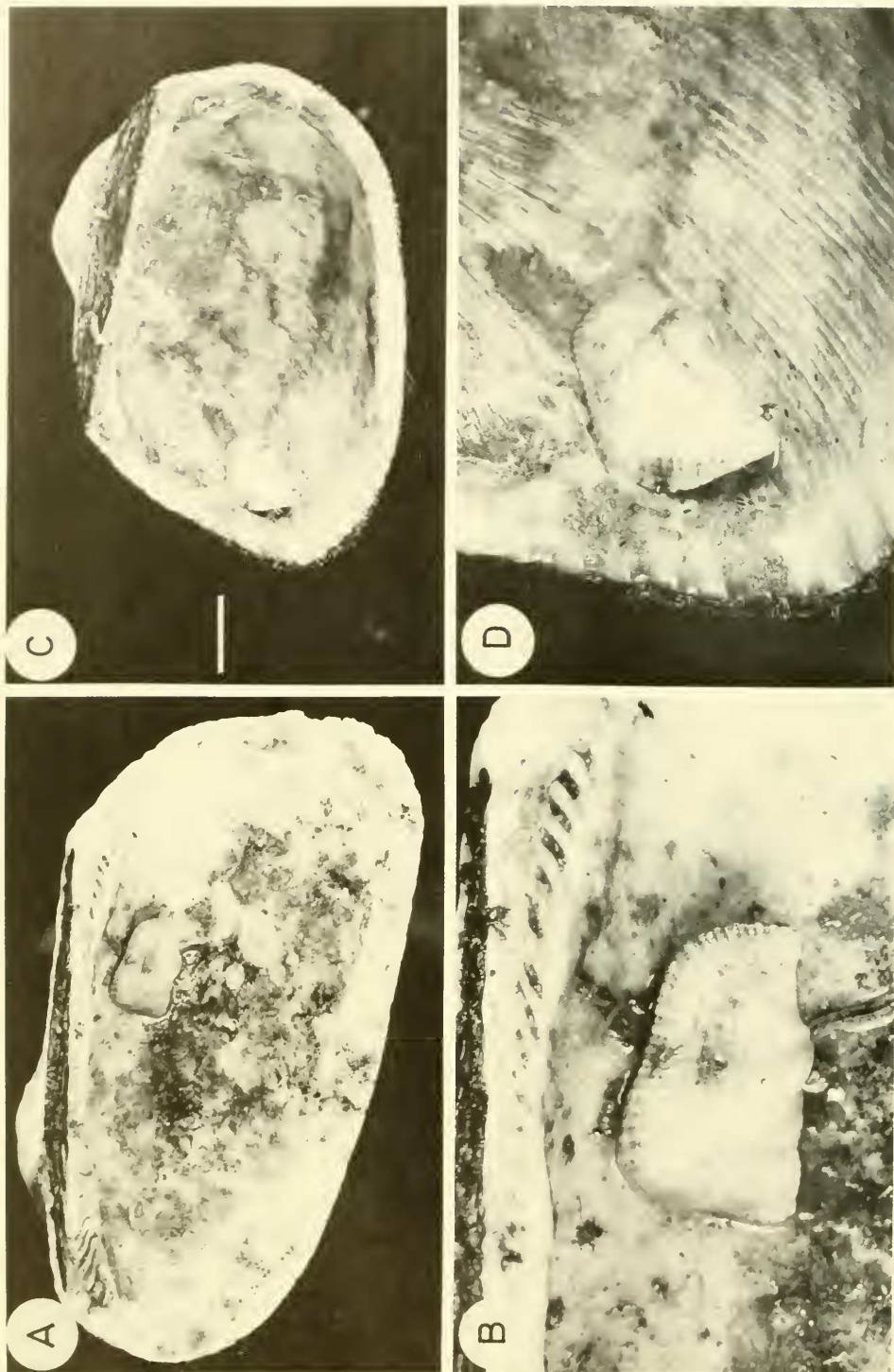
FIG. 1. *Trisidos semitorta*. Low (A, C) and high (B, D) power photographs of two juvenile specimens attached to the internal surface of shell valves of (A, B) adult *T. semitorta* and (C, D) *Anadara antiquata*. Scale = 1 cm.

It appears that the posterior end has been twisted clockwise, the posterior part of the sagittal plane turned through approximately 45° in *T. semitorta* and almost 90° in *T. tortuosa*. The animal, though lying approximately vertically disposed in the sand with the anterior dorsoventral axis of the shell at right angles to the sediment-water interface, has its posterior margin lying approximately flush with the sand. The right valve, located underneath the left, is buried. In both, but more noticeably in *T. tortuosa,* the posterior edge of the left valve projects beyond the margin of the right valve. The animal is slightly tilted in the sand, anterior end down, so that only the posterior face of the left valve is seen in life.

The anterior end is not (except coincidentally) involved in the twisting process and thus the anterior region of the hinge plate remains vertically aligned whereas the hinge plate is twisted posteriorly and the posterior teeth interlock in a different plane to those anterior. Because of the twisting, the posterior adductor acts at a different angle to that of the anterior and may augment the function of the hinge teeth in preventing shear (McGhee, 1978). The dorso-ventral axis of the shell, through the ligament and byssus, constitutes the fixed pivot point around which posterior twisting occurs. Tevesz & Carter (1979) considered the hinge axis alone to be the pivotal point while McGhee (1978) considered it the byssus. The ligament is straight, though much larger in *T. semitorta* than *T. tortuosa*. *T. tortuosa* is more delicate than *T. semitorta*. In *T. semitorta* the shell is delicately ribbed, though this is often masked by the thick, fibrous periostracum and by heavy erosion of the left valve posteriorly. *T. semitorta* also possesses a weak postero-ventral sulcus extending from the umbo. This is most noticeable in the left valve. In *T. tortuosa*, the sulcus is much more sharply defined and angles the left valve so that the posterior face lies at right angles both to the remainder of the valve and to the sediment-water interface. As a result of the twisting process, the ventral margin of both species is sinusoidally curved. There is no trace of a byssal notch or ventral indentation, though Newell (1969) considers this characteristic of the subfamily. In *T. tortuosa*, but not *T. semitorta*, both posterior and anterior halves of the shell are laterally compressed, emphasizing the angularity of the shell.

Juveniles of *T. semitorta* are byssally attached, though whether this is also true of *T. tortuosa* is unknown but probable. Fig. 5
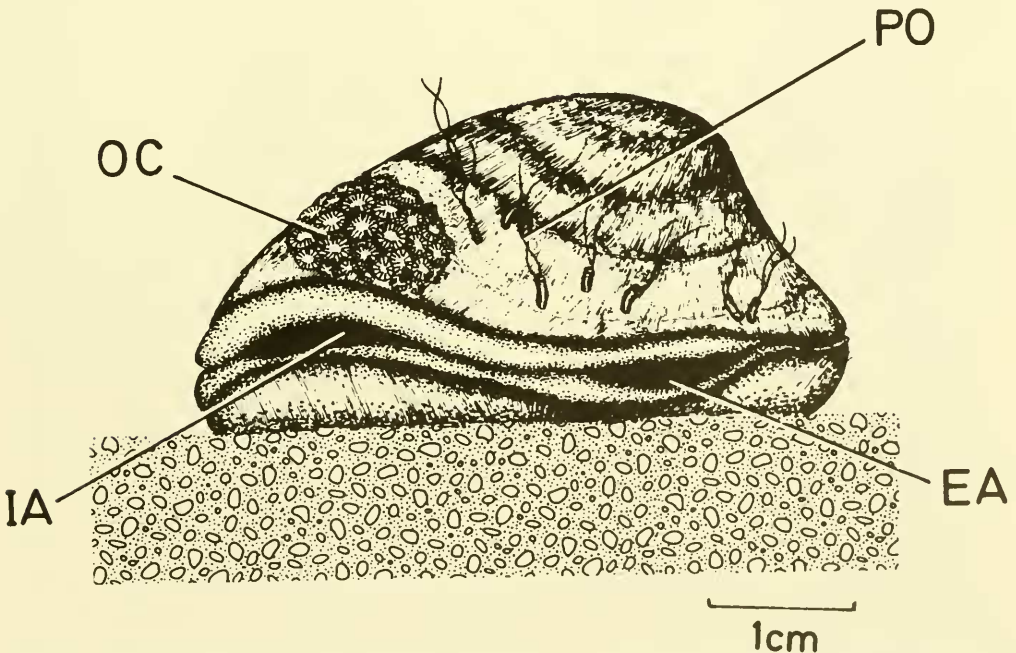

FIG. 2. *Trisidos semitorta.* A posterior view of the animal in a natural position in the sand with the inhalant and exhalant apertures open. For abbreviations see p. 376.
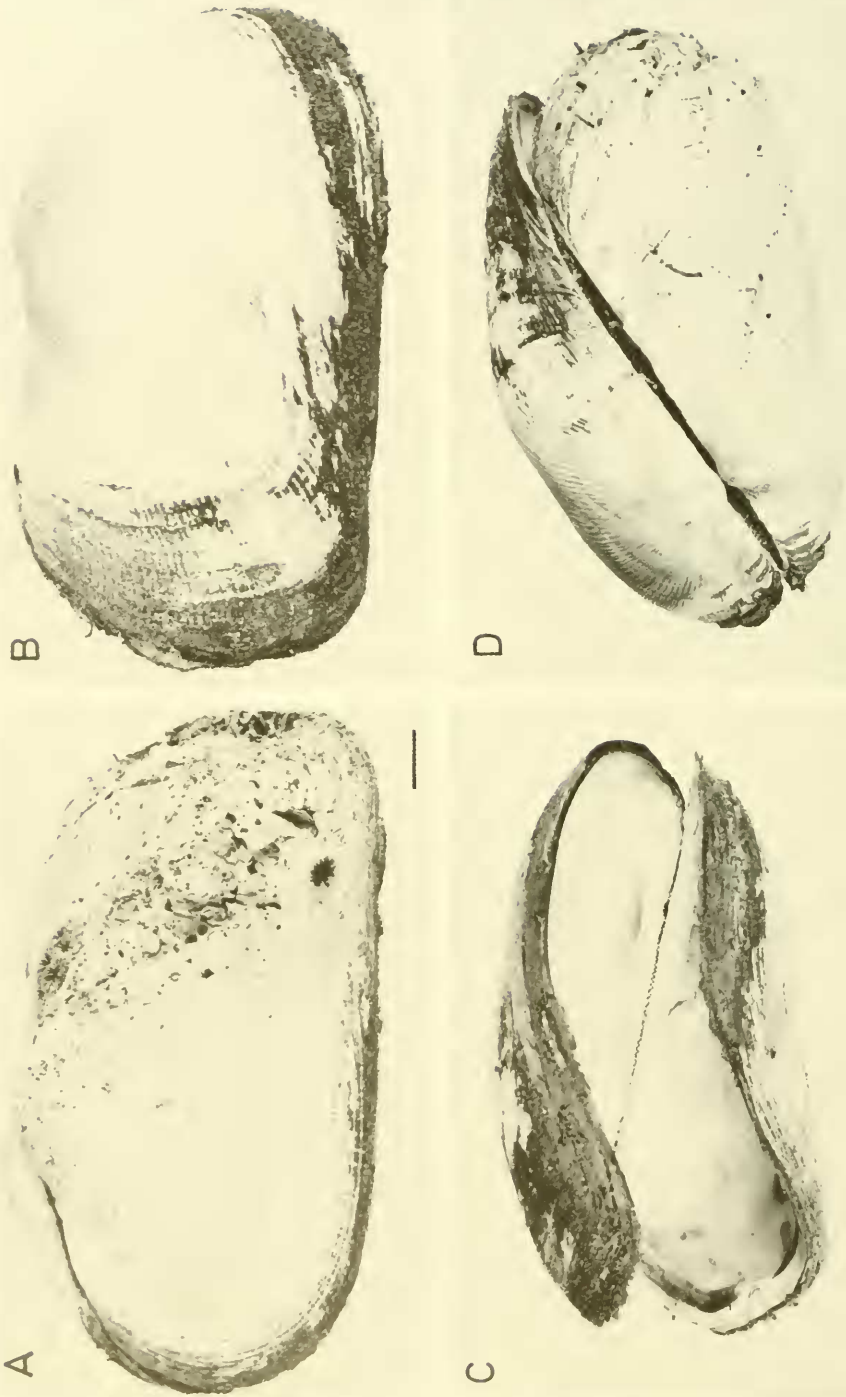
FIG. 3. *Trisidos semitorta*. The shell viewed from A, the left; B, the right; C, the ventral and D, the dorsal aspects. Scale = 1 cm.

shows dorsal and ventral views of a juvenile specimen of *T. tortuosa* 11 mm long and an adult 73 mm long. It can be seen that the juvenile is less twisted than the adult, the twisting process progressively influencing shell form with age and growth. Although no newly settled individuals have been seen, growth probably proceeds from an equilateral body plan. Neither juvenile *T. semitorta* nor *T. tortuosa* possess a byssal notch, though the former at least is byssally attached when young and possesses a ventral byssal indentation (McGhee, 1978). This results in a slight heteromyarian form with an inflated posterior region relative to the anterior, the inequilaterality being enhanced by the byssal indentation. Figs. 1 and 6A of a young specimen of *T. semitorta*, 13 mm long, demonstrate the low degree of twisting. The shell, somewhat inequivalve, has the characteristics of a nestling

bivalve with relatively reduced anterior and inflated posterior shell slopes. The greatest shell width is dorsal to the dorso-ventral axis of the shell so that contraction of the byssal retractor muscles effectively serves to pull the animal down into the inner surface of large bivalve shells. The inflated posterior region of the shell increases the size of the apertures to the water above, thereby enhancing exchange and is typical of nestling species, e.g. *Philobrya* (Limopsacea), *Neogaimardia* (Cyamiacea) and *Trapezium* (Arcticacea) (Morton, 1978; 1979a, b). The similarity between juveniles of *T. tortuosa* and *T. semitorta* is evidence for similar life styles (Fig. 6). Conversely, the adults are dissimilar, though both exhibit twisting. Clearly, the constraints of the juvenile niche are responsible for a uniformity of body form that subsequently, in adult freedom, achieves individual character.
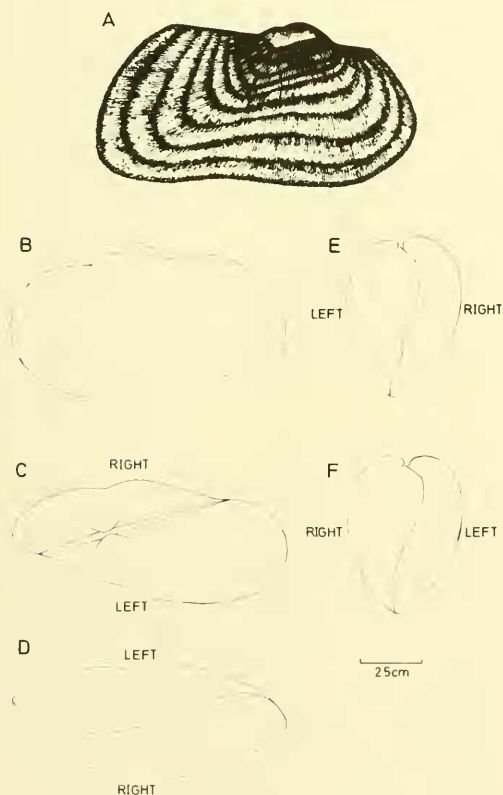

FIG. 4. *Trisidos semitorta*. The adult shell viewed from various aspects. A, the right valve; B, the left valve; C, dorsal aspect; D, ventral aspect; E, posterior aspect; F, anterior aspect.
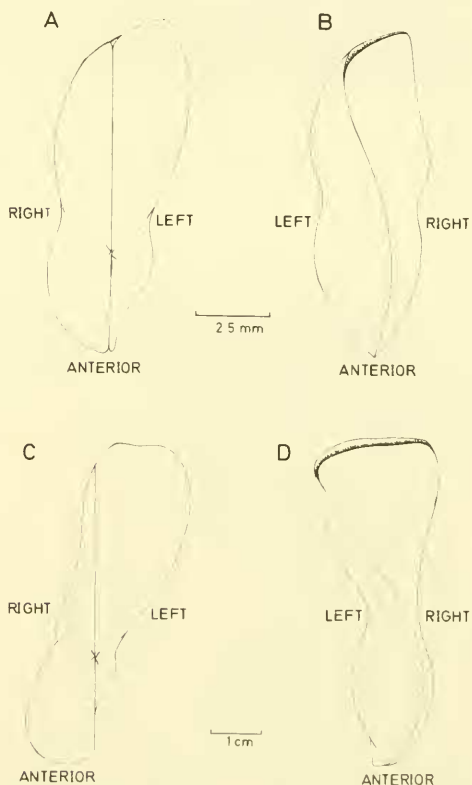
FIG. 5. *Trisidos tortuosa*. A and B, dorsal and ventral views of a juvenile; C and D, dorsal and ventral views of an adult.
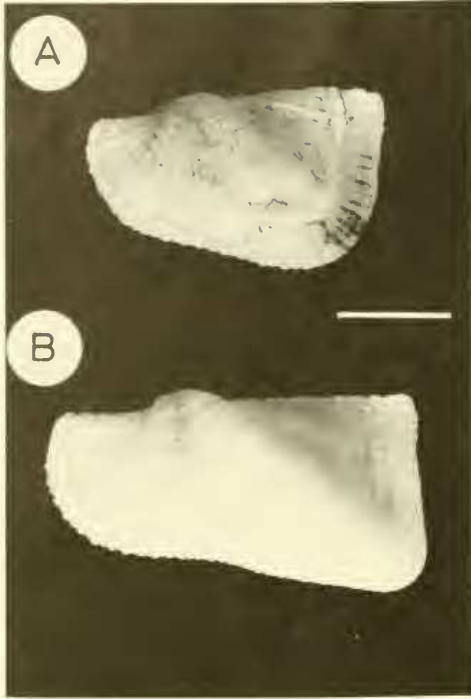
FIG. 6. The left shell valves of juvenile specimens of A, *Trisidos semitorta* and B, *T. tortuosa*. Scale = 5 mm.

The musculature

Anterior and posterior adductor muscles are present (Figs. 11 and 17), the former being smaller and more dorsal than the latter. Inequality of the adult adductors represents a continuation of the juvenile condition. Both adductors are divided into slow (AA(S); PA(S)) and quick (AA(Q); PA(Q)) components of approximately equal size.

Ventral to the anterior adductor, a pair of anterior pedal protractor muscles (APP) extend into the visceral mass. Similarly, from the postero-dorsal edge of the anterior adductor is attached a pair of anterior pedal retractor muscles (APR). Left and right anterior pedal retractors and protractors are of equal size.

How twisting in *Trisidos* is achieved has never been elucidated. Anterior to the posterior adductor muscle of *T. semitorta* is a pair of posterior pedal retractor muscles (PPR). Figs. 7A and 8 show that the left muscle (PPR(L)) is large, with a wide area of attachment and passes into the visceral mass and foot to largely assume responsibility for posterior retraction of the foot both on the left and right sides. The right posterior pedal retractor (PPR(R)) is small, with a small attachment area and is located anterior to the left retractor and its muscle blocks extend only a small way into the visceral mass.

The situation in *T. tortuosa* is similar (Fig. 7B) but exaggerated, i.e. the right posterior pedal retractor is minute in comparison with the left and as such is unusual, seen only in *Trisidos* (as far as is known), and results in the posterior twisting of the shell.

The mantle

The mantle is very thick and fleshy, tinted brown, with no mantle fusion. Posteriorly, the left and right mantle lobes are apposed so that inhalant and exhalant apertures are formed. When the animal is lying in sand (Fig. 2, IA, EA), these are clearly visible. The large foot can protrude mid-ventrally from between the mantle lobes to effect digging.

In transverse section (Fig. 9), the mantle epithelia are widely separate and the enclosed haemocoel divisible into two components. Beneath the inner epithelium (IME) is an extensive haemocoel crossed by a few obliquely oriented muscle fibres (OFM) that presumably maintain the turgidity of the haemocoel, perhaps ensuring it is not overfilled with blood. This cavity contains numerous amoebocytes. Similar oblique muscle fibres occur in the spacious haemocoel in the mantle of the anomalodesmatan *Pholadomya candida* (Morton, 1980). Beneath this region is a further haemocoel abutting the outer mantle epithelium (OME) and crossed by many transverse fibres (TFM). Clearly, this haemocoel can expand very little.

Throughout the mantle occur large numbers of cells (SC), termed secretory cells, each apparently discharging at an epithelium and containing granules staining bright red in Ehrlich's haematoxylin and eosin and either red or green in Mallory's triple stain. These cells, a maximum of some 25 μm in diameter, are also found throughout the body, being particularly common in those epithelia in contact with the mantle cavity and in the gut epithelia.

The mantle margin (Fig. 10) comprises three folds (Yonge, 1957), the inner (IMF) being the largest and the middle fold (MMF) extremely reduced. Discharging onto the general outer surface of the inner fold are many
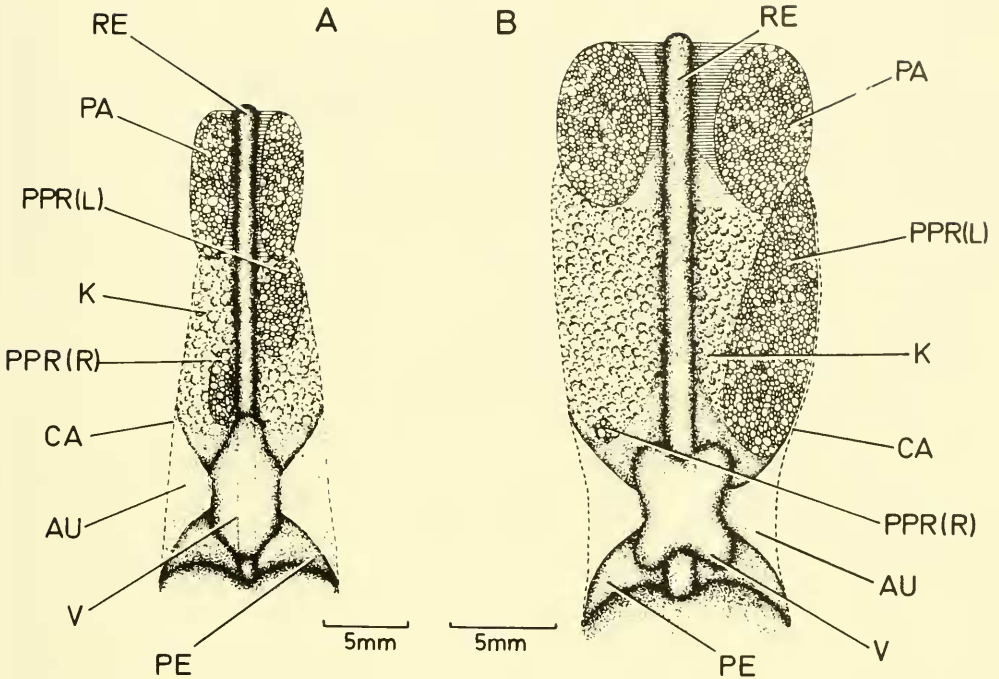
FIG. 7. Dorsal views of the pericardium of A, *Trisidos semitorta*; B, *T. tortuosa*. For abbreviations see p. 376.

subepithelial gland cells (PG), staining blue/green in Mallory's triple stain and pale red in Ehrlich's haematoxylin and eosin. A mucin probably is produced. Most of the branches of the pallial retractor muscle (PRM) penetrate the inner fold. Beneath the surfaces of the outer fold (OMF), which is subdivided into two sub-folds, occur large numbers of the subepithelial secretory cells (SC) noted above. The periostracum (P) is thin.

The ciliary currents of the mantle

Waste material landing on the surface of the mantle is rejected posteriorly. On each lobe (Fig. 11), a major rejection tract commences ventral to the anterior adductor muscle, extends postero-ventrally and then turns in a postero-dorsal direction so that unwanted material is eventually discharged via the exhalant aperture. This is achieved largely by ciliary means, as in other arcids (Lim, 1966) and mytilids (Morton, 1973). This major rejection tract is fed from the dorsal and ventral areas of the mantle by, respectively, down-
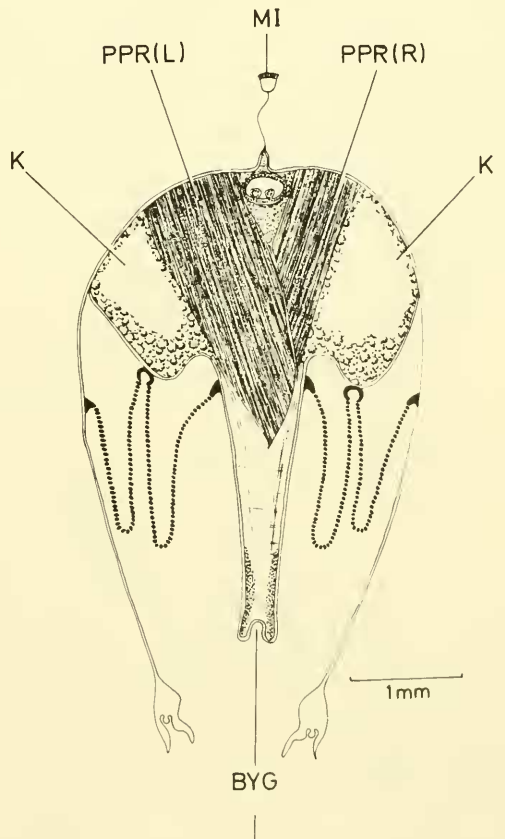

FIG. 8. *Trisidos semitorta*. Transverse section through the posterior pedal retractor muscle. For abbreviations see p. 376.
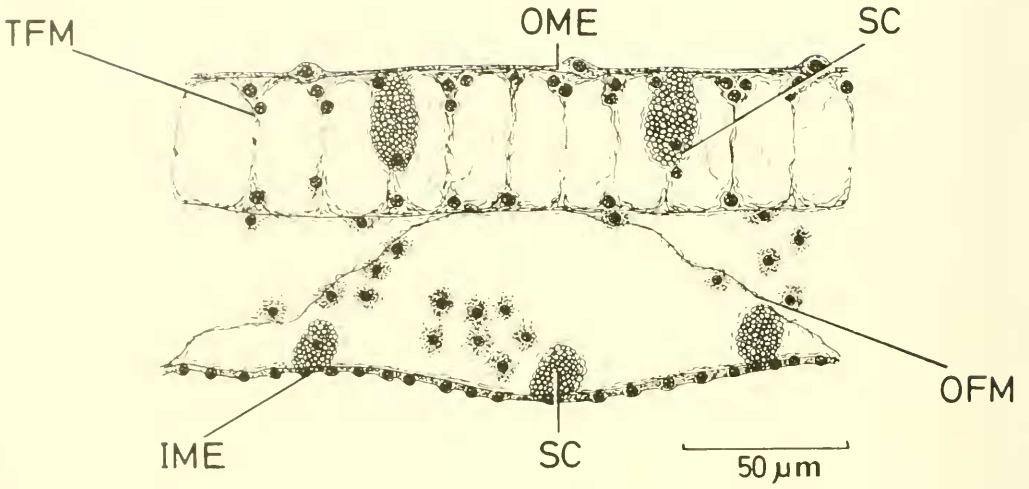
TFM   OME   SC

OFM

IME   SC

50 μm

FIG. 9. *Trisidos semitorta*. Section through the general mantle. For abbreviations see p. 376.

PRM

50 μm

SC

IMF

OMF
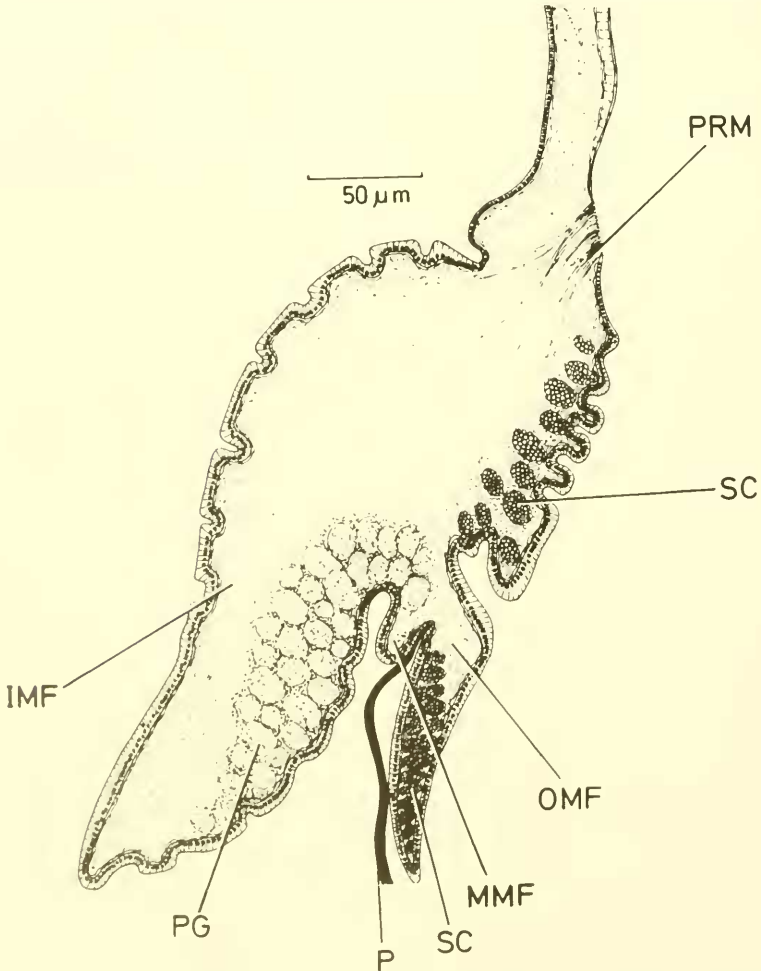
PG   MMF

P   SC

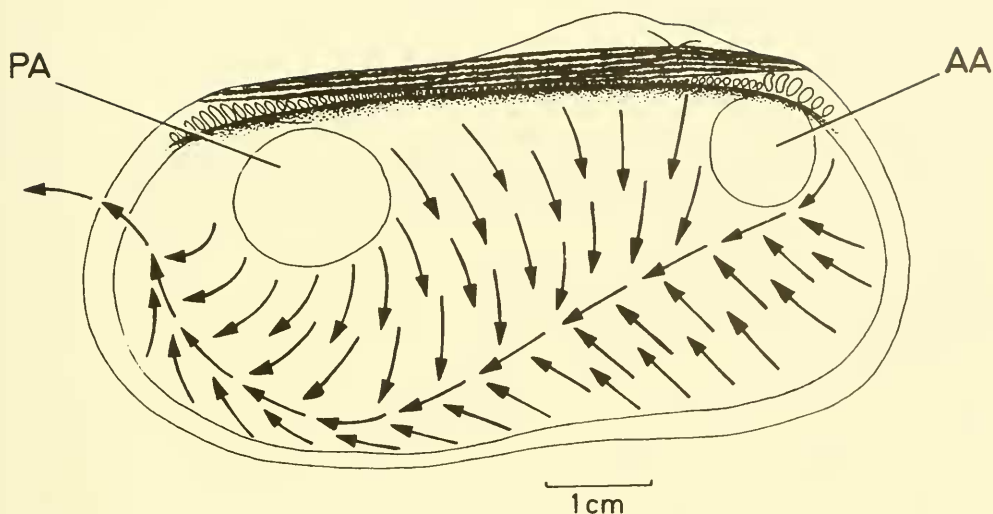FIG. 10. *Trisidos semitorta*. Transverse section through the ventral mantle margin. For abbreviations see p. 376.

FIG. 11. *Trisidos semitorta*. The ciliary rejection currents of the left mantle lobe. For abbreviations see p. 376.
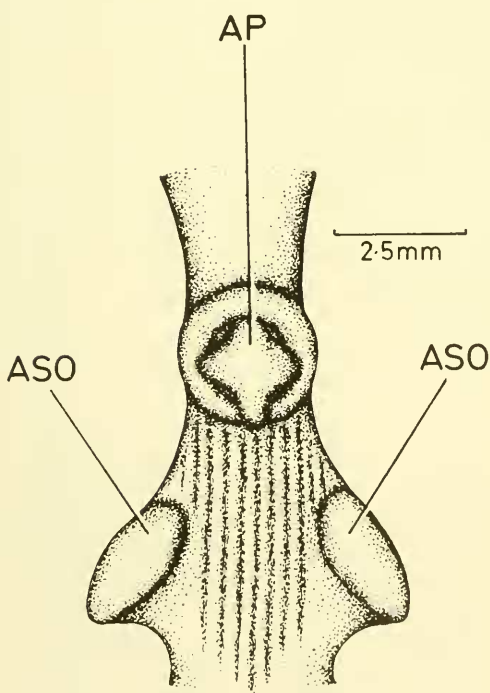

FIG. 12. *Trisidos semitorta*. Surface view of the anus and abdominal sense organs located beneath the posterior adductor muscle. For abbreviations see p. 376.

wardly and upwardly beating cilia. The ciliary currents are extremely strong.

The abdominal sense organs

Members of the Arcacea typically possess a pair of large abdominal sense organs (Heath, 1941) (Fig. 12, ASO) located close to the anus with its anal papilla (AP) and in close proximity to the postero-ventral face of the posterior adductor muscle. Heath (1941) has shown that in *T. tortuosa*, along with the very great asymmetry of the valves, the right abdominal sense organ is markedly larger than that of the left. This is not so in the less twisted *T. semitorta*.

In section (Fig. 13) large numbers of secretory cells (SC) (earlier described) are present in the sense organs, apparently being discharged from the epithelium. The epithelium comprises a very regular row of vertically aligned cells with long (8 μm) nuclei (SEC), located just beneath the outer cell membrane. Beneath occur large numbers of round nuclei (NU), some 4 μm in diameter and forming a layer 16 μm thick, and beneath this again is a zone 4 μm thick comprising vertically aligned, fine fibrils (NF) overlying a layer (4 μm) of horizontally aligned nervous tissue (N). It would seem that the fibrils arise from the nerve and extend upwards towards the vertically aligned apical nuclei, but this con-

A

100 μm

B

SEC   NU

N   SC
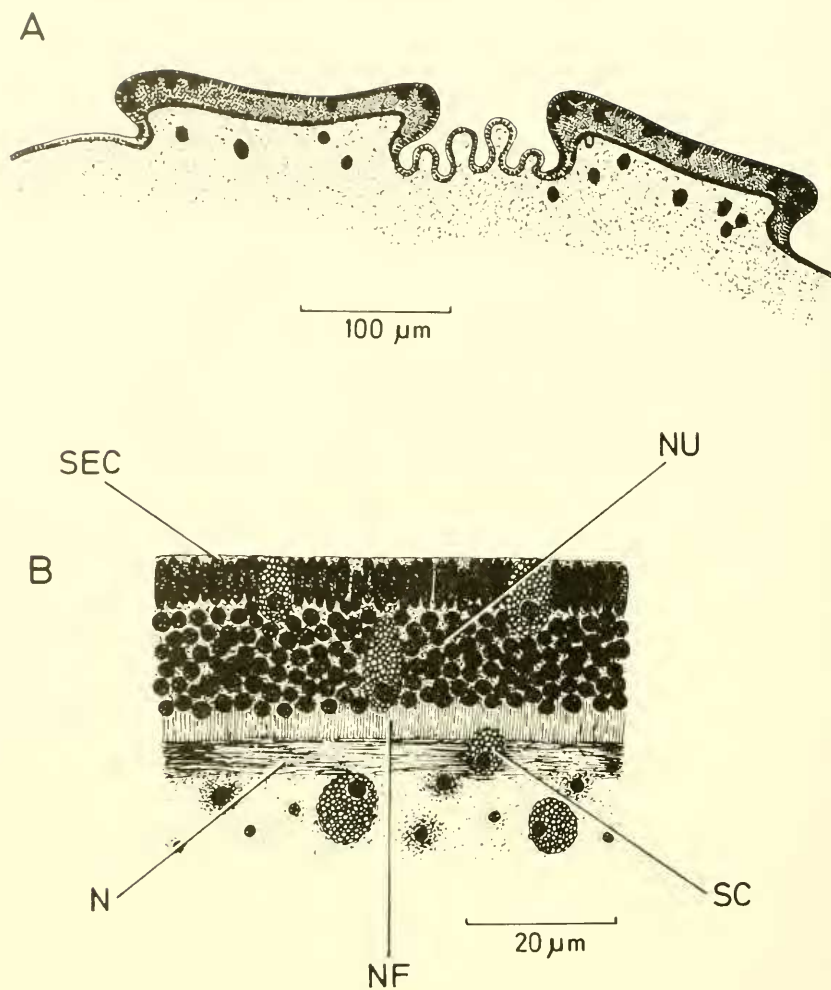
20 μm

NF

FIG. 13. *Trisidos semitorta*. Low (A) and high (B) power sections through the abdominal sense organ(s). For abbreviations see p. 376.

nection is obscured by the mass of intervening nuclei.

The ctenidia

The ctenidia of *T. semitorta* (Fig. 14) comprise two equal demibranchs: left and right ctenidia are similarly equal, i.e. valve inequality does not affect gill dimensions. Gill ciliation is of Type B(1a) (Atkins, 1937b), typical of the Arcacea and Limopsacea (Atkins, 1937a; Lim, 1966; Morton, 1978). Acceptance tracts are located in the ctenidial axis and in the junctions between the ascending lamella of the inner (ID) and outer (OD) demibranchs

with the visceral mass and mantle, respectively. The ventral marginal grooves pass large particles posteriorly to be rejected from between the posterior borders of the mantle along with pseudofaeces collected by the visceral mass and mantle. The posterior extremities of the ctenidia are supported by a thick, muscular, suspensory membrane which gives this region great mobility. The ctenidia, with acceptance and rejection tracts separately located, act as primary sorting mechanisms, facilitated by the ciliation of the gill filament.

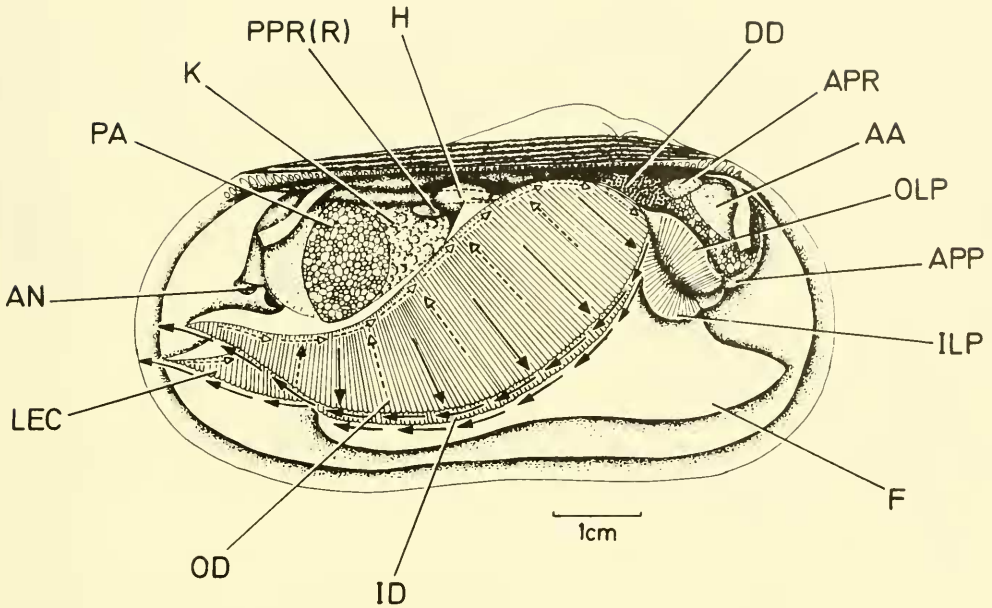In transverse section (Fig. 15), each filament has an apical crown of some six cells,

FIG. 14. *Trisidos semitorta.* The organs of the mantle cavity as seen from the right side after removal of the right shell valve and mantle lobe. For abbreviations see p. 376.

each ciliated. The cilia are arranged in three vertical rows. A central row of coarse frontal cilia (CFC) 5–6 μm long, is flanked by rows of fine frontal cilia (FFC) 3–4 μm long. Lateral to the fine frontal ciliated cells is another cell with a long (8–10 μm), stiff cilium designated the latero-frontal cilium (LFC) by Atkins (1937a). Lateral again is a secretory cell (FGC), probably producing mucus, and a series of, typically, three cells possessing long (12 μm) lateral cilia (LC) responsible for creating the flow of water through the ctenidium and another large secretory cell (FGC), again probably producing mucus. The apex of the filament is supported by "chitinous" rods (CR); and the base of the filament enclosing the filament blood vessel is long, thin and composed of narrow cells, the two sides cross-linked by transverse fibres (TF).

The labial palps

The labial palps (Fig. 14, ILP, OLP) are located on the postero-ventral face of the anterior adductor muscle. Only the tips of the demibranchs extend between the palps. The ctenidial-labial palp junction is of category 3 (Stasek, 1963), typical of the Arcacea. The palps of *T. semitorta* have a parallel series of ridges and grooves on their inner surfaces oriented at approximately right angles to the oral groove.

Very fine particles quickly pass over the crests of the palps towards the mouth (Fig. 16). Large particles pass into the depths of the troughs between ridges and are transported outwards towards the palp margin where they fall off onto either the visceral mass or the mantle and are thence removed. On the oral surfaces of the crests, the ciliary currents beat downwards whereas on the aboral surface they generally beat upwards, out of the troughs. On this surface are a number of laterally directed resorting currents. Resorting currents also exist on the crests of each ridge and these re-subject particles of intermediate size to either the acceptance or the rejection currents. In this process, apposition or parting of the crests ensures that virtually all or very little material is accepted or rejected.

The foot and byssus

The foot of the adult (Figs. 14 and 17, F) is antero-posteriorly elongate with a rather small digging "toe." There is a long, ventral byssal groove (BYG) but no byssus, though adult *T.*
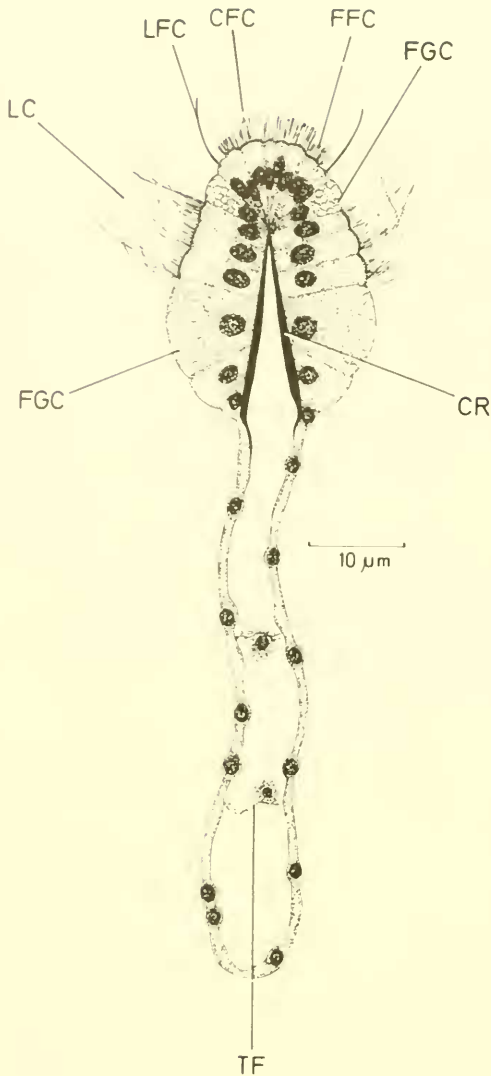
FIG. 15. *Trisidos semitorta.* A transverse section through a single ctenidial filament. For abbreviations see p. 376.

tortuosa possesses a long, thin byssus (McGhee, 1978; Tevesz & Carter, 1979).

Sections of juvenile *T. semitorta* (Fig. 18) having a stout byssus (BY) show the byssal roots radiating deeply into the visceral mass. The epithelium of the byssal groove is surrounded by dense numbers of subepithelial cells of the byssal gland (BG) which stain bright red in both Ehrlich's haematoxylin and eosin and Mallory's triple stain.

Ventrally the foot contains another exten- sive sub-epithelial gland (PEG) that is not in- volved in secretion of the byssus but which may be responsible for the mucus copiously produced here. The cells are basophilic and stain red in Mallory's triple stain.

The ciliary currents of the visceral mass

The ciliary currents of the visceral mass (Fig. 14) complement those of the mantle. Thus a major rejection tract on each side of the body commences ventral to the anterior adductor muscle and extends to the postero- ventral edge of the visceral mass. Cilia on the visceral mass beat towards it. There are few currents supplying it from the foot. Waste ma- terial arriving at the posterior edge of the vis- ceral mass falls off, largely onto the right man- tle lobe.

The alimentary canal

The mouth, located on the ventral face of the anterior adductor muscle, opens to the oesophagus which passes dorsally to merge with the stomach. In transverse section (Fig. 19A) the oesophagus of a small juvenile spec- imen comprises a tube some 160 μm in di- ameter composed of a columnar epithelium, approximately 60–80 μm tall with cilia 10 μm long. It is thrown into four longitudinal folds, though this number may increase in the adult, as in *T. tortuosa* (Heath, 1941, pl. 10, fig. 4).

From the postero-ventral wall of the stom- ach the conjoined style sac and mid-gut ex- tends vertically down into the visceral mass. Transverse sections (Fig. 19B) show that the greater part of the style sac is lined by a col- umnar epithelium termed the A cell layer (A) consisting of cells 30 μm tall with a nucleus 8 μm in diameter and a thick border of cilia 10 μm long. In the Arcacea major and minor typhlosoles largely serve to separate the mid- gut and style sac. In section they comprise thin, elongate cells some 100 μm tall, pos- sessing a centrally located, similarly elongate (6 μm) nucleus and with a fringe of cilia 8 μm long. Internal to each typhlosole (the B (major) and B_1 (minor) cell layers) is a C cell layer (C), forming part of the epithelial lining of the mid-gut. The cells are approximately 65 μm tall each with a fringe of stiff, bristle- like cilia, 4 μm long, that characterize this re- gion (Henschen, 1904; Kato & Kubomura, 1954; Morton, 1969). The remainder of the mid-gut epithelium comprises the D cell layer (D) of cuboid cells 16 μm tall and with cilia 8 μm long.
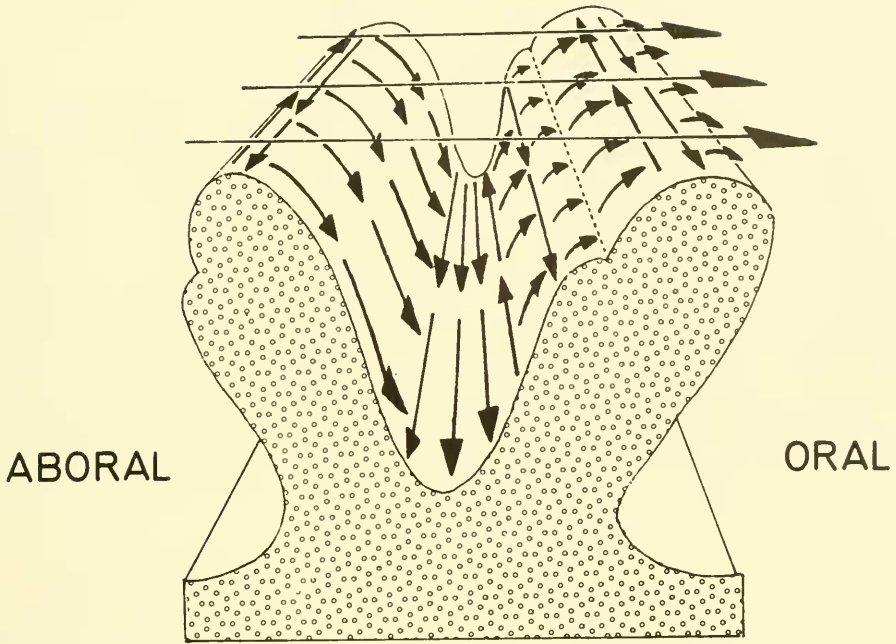
FIG. 16. *Trisidos semitorta*. The ciliary currents of two ridges and a groove of the labial palps.
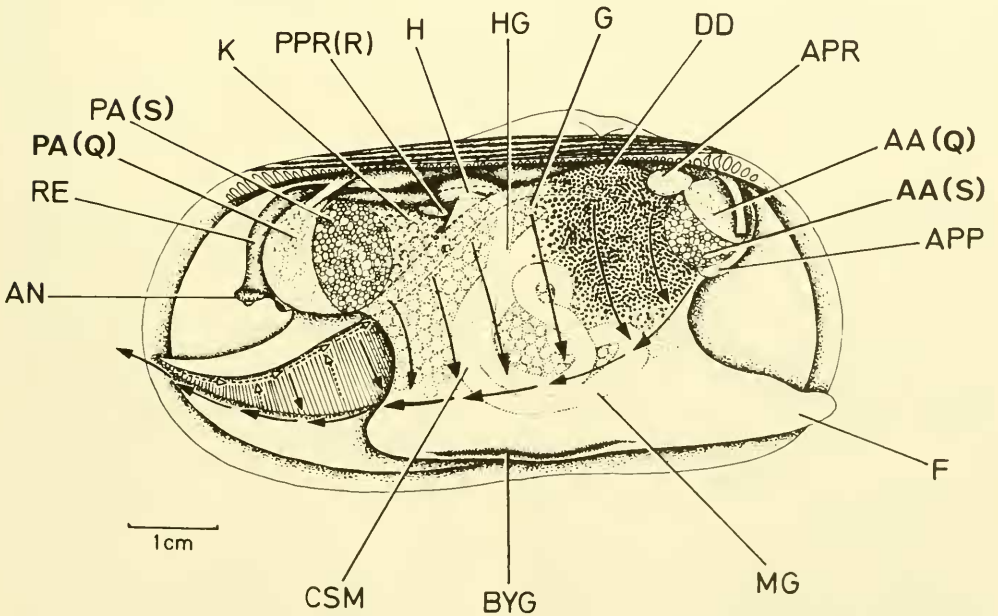

FIG. 17. *Trisidos semitorta*. The structure and ciliary currents of the visceral mass as seen from the right side after removal of the right shell valve, mantle lobe and ctenidium. For abbreviations see p. 376.
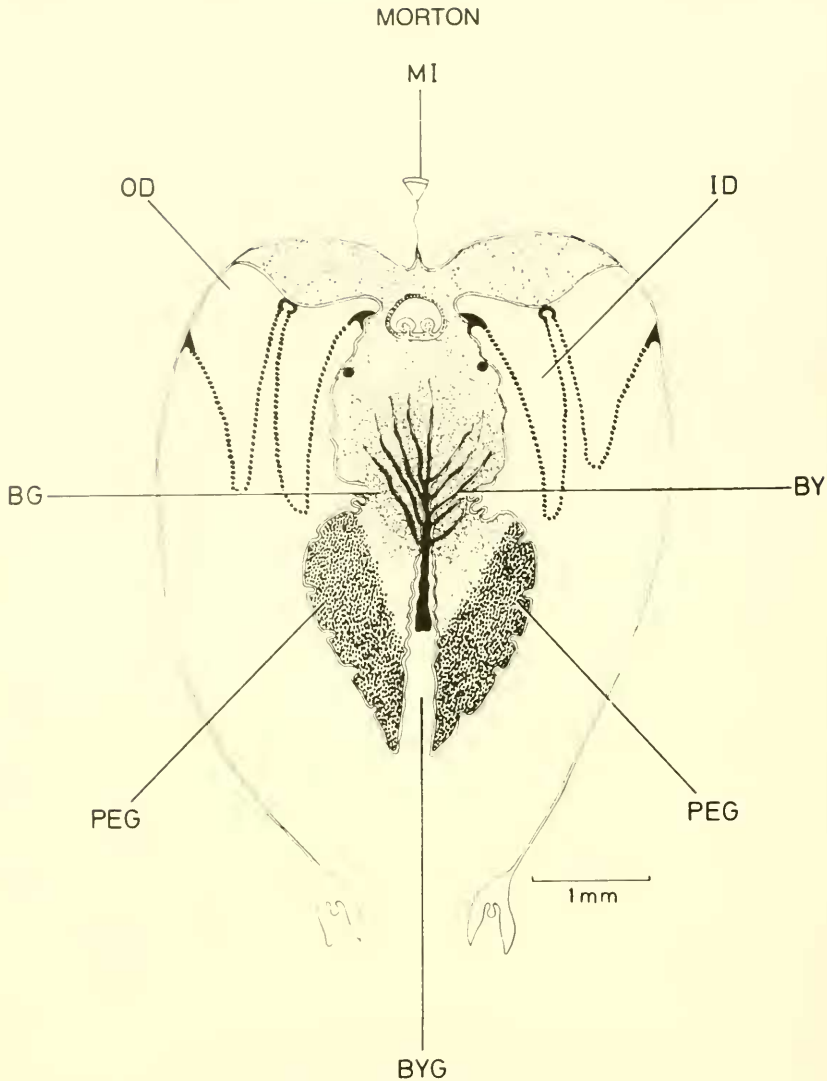
FIG. 18. *Trisidos semitorta*. A transverse section through the visceral mass of a juvenile in the region of the byssus. For abbreviations see p. 376.

In the ventral region of the visceral mass (Fig. 17), the mid-gut (MG) is separate from the style sac and coils before passing dorsally as the hind-gut (HG). In transverse section (Fig. 19C) the mid-gut is a circular tube 200 μm in diameter with a single typhlosole comprising cells 80 μm tall with cilia 14 μm long. The remainder of the mid-gut epithelium comprises a columnar epithelium 40 μm tall similarly ciliated. The hind-gut gives rise to the rectum. In section (Fig. 19D) the rectum comprises a tube 140 μm in diameter and comprising cells 20 μm tall with cilia 6 μm long. In the rectum the typhlosole divides into two ventral, longitudinal ridges. The rectum (Fig. 17, RE) penetrates the ventricle of the heart (H), passes between the posterior pedal retractor muscles (PPR) and thus also between the kidneys (K) and over the posterior adductor muscle (PA) to terminate on the postero-ventral face of this muscle at an anus (AN) with a distinctive anal papilla.

The stomach

The large stomach (Fig. 20) lies ventral to the anterior region of the hinge plate and is of Type III (Purchon, 1957). The terminology
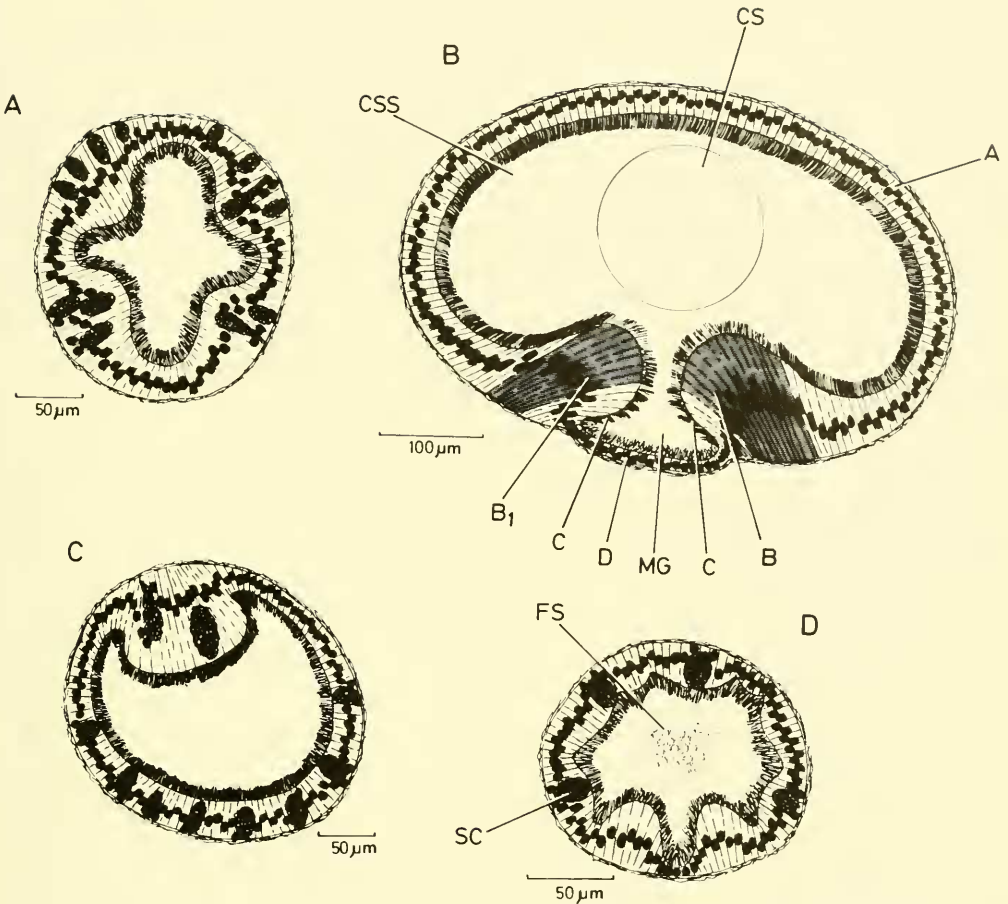
FIG. 19. *Trisidos semitorta*. Transverse sections through (A), the oesophagus; (B), the conjoined style sac and mid gut; (C), the mid gut; (D), the rectum. For abbreviations see p. 376.

used in this description follows that of Purchon. The minor typhlosole terminates soon after emerging into the stomach. The major typhlosole extends across the floor of the stomach from right to left to terminate in a capacious food sorting caecum (FC). The food sorting caecum extends dorsal to the entrance of the oesophagus (O). The major typhlosole has on its right side the intestinal groove (IG) which transports waste material into the mid-gut. In the food sorting caecum is a very large sorting area (SA). Between each of the adjacent ridges of the sorting area is an aperture which leads into a component part of the digestive diverticula (DDD). A ridge dorsal to the row of sorting ridges carries material into the caecum. There is, in addition to the intestinal groove, a further ridge (R) carrying recycled material to the dorsal hood (DH)

from where it is probably returned to the head of the style (CS) rotating against the gastric shield (GS). The latter is very small in relation to the size of the stomach and is located on the postero-dorsal wall. It sends spurs into the dorsal hood and the left pouch (LP). From the left pouch a series of ducts opens into the digestive diverticula. Particles settling on the surface of the major typhlosole are swept towards the left pouch and the ridge leading to the dorsal hood.

The pericardium and associated organs

The heart (Figs. 7 and 21) comprises a single ventricle (V) and paired lateral auricles (AU). From the posterior wall of the pericardium (Fig. 21, PE), paired reno-pericardial apertures (RPA) open into the paired kidneys
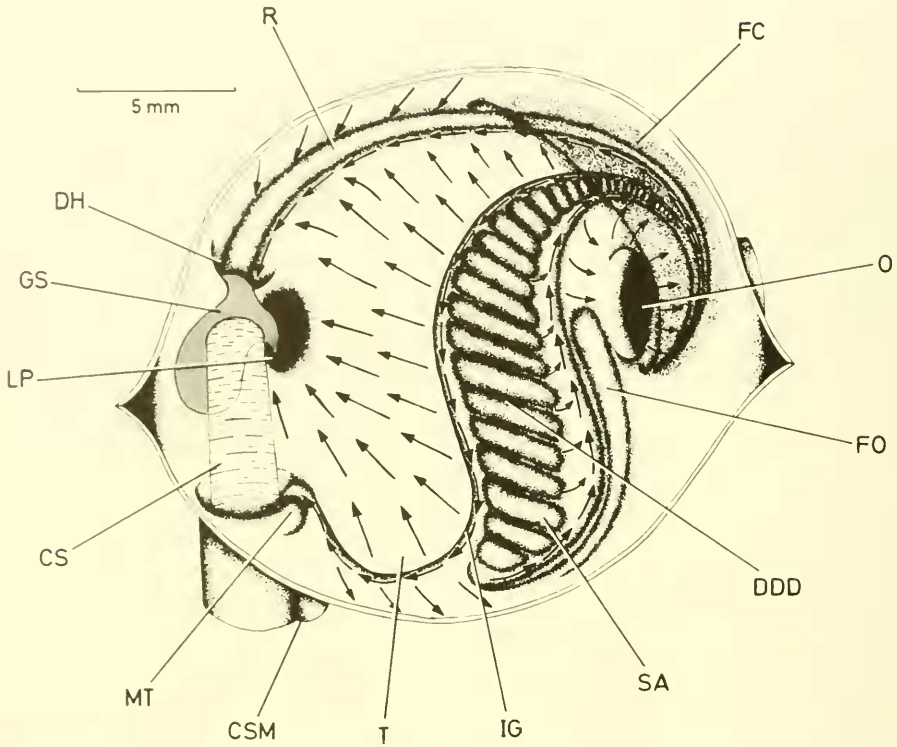
FIG. 20. *Trisidos semitorta.* The internal structure and ciliary currents of the stomach after opening by an incision in the right wall. For abbreviations see p. 376.
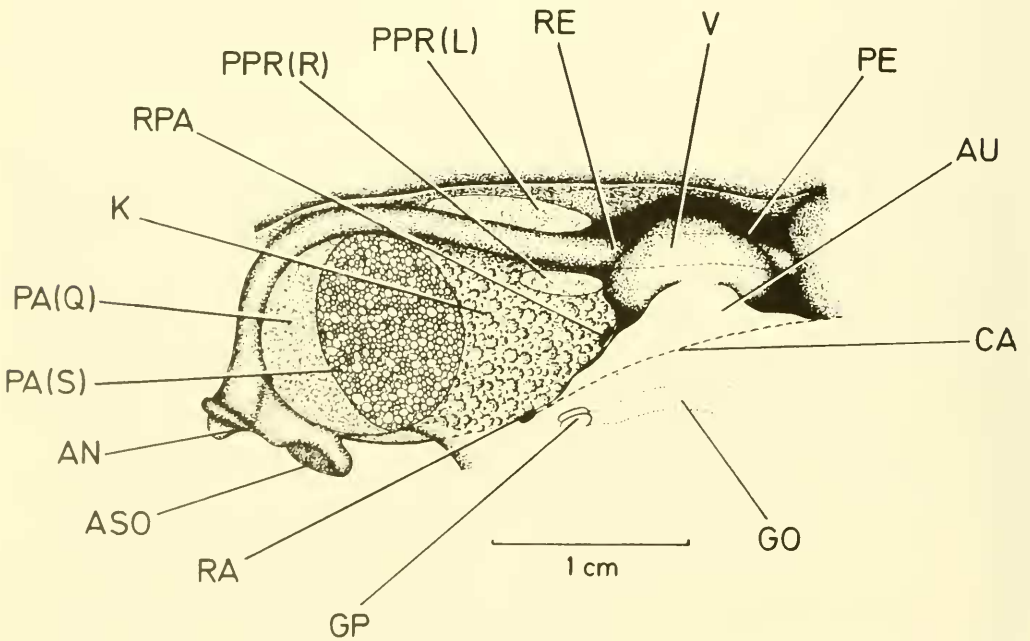

FIG. 21. *Trisidos semitorta.* The organs of the pericardium as seen from the right side. For abbreviations see p. 376.

(K). The kidneys lie posterior to the pericardium and lateral to the posterior pedal retractor muscles (Fig. 8). In section the kidneys comprise a ventral series of tubules, but dorsally there are few tubule cells as described for *T. tortuosa* (Health, 1941, pl. 11, fig. 3). The renal apertures (RA) discharge into the suprabranchial chamber.

Close to the renal aperture is the gonopore (GP), which has thick fleshy lips. In *T. tortuosa* gonopore and renal aperture are joined (Heath, 1941).

DISCUSSION

The shell of *Trisidos,* especially *T. tortuosa,* has been discussed previously (Makiyama, 1931; McGhee, 1978; Tevesz & Carter, 1979). *Trisidos* is unusual in being the only known extant twisted bivalve genus. In most morphological respects, *Trisidos semitorta* is a typical ark. Thus, the ctenidia and labial palps are little modified, the general disposition of the mantle and organs of the mantle cavity and visceral mass are typically arcacean. The ciliary rejection currents of the mantle cavity, whilst also arcacean, are modified to enable the adult, partially buried in soft deposits, to remove large amounts of sediment that may enter the largely open mantle cavity. The shell is eroded posteriorly on the left valve only, the posterior end lying flush with the sediment-water interface and the right valve being wholly buried. The anterior end lies vertical to the surface. The structure and position of the posterior abdominal sense organs suggests a photoreceptive function, there being no sensory cilia suitable for monitoring water flow. *T. kiyonoi* and *T. tortuosa* live in the same way as *T. semitorta* (Makiyama, 1931; Tevesz & Carter, 1979). Twisting does not seem to have any effect upon the distribution or size of the organs of the mantle cavity. Thus in *T. semitorta* left and right ctenidia, mantle lobes and labial palps are of approximately the same size in marked contrast to the left and right inequality seen in the tangentially coiled Chamidae and Cleidothaeridae (Yonge, 1967; Morton, 1974) and to a lesser extent in the markedly inequivalve *Claudiconcha japonica* (Morton, 1977). In *T. tortuosa,* however, left and right abdominal organs are of notably different size (Heath, 1941)—this is not so in *T. semitorta.* Also, the left and right posterior pedal retractor muscles are of different sizes; this influences slightly the size of left and right kidneys.

Tevesz & Carter (1979) suggest that *Trisidos* is more probably evolved from a morphologically less specialized representative of the Arcinae similar to the modern *Barbatia.* They argue that because of its relatively efficient ligament (Thomas, 1976) and streamlined shape a *Barbatia*-like ancestor was preadapted for the evolution of a shallow burrowing life habit. Superficially it would seem more reasonable to derive the burrowing, abyssate *Trisidos* from a shallow burrowing limopsacean (Limopsidae and Glycymerididae), but Thomas (1976) has shown that the duplivincular ligament of these is inherently weak, arguing for morphological conservatism and not conducive to evolutionary diversification.

Purchon (1957) describes stomachs of representatives of the Arcidae and Glycymerididae, and it is clear that a *Barbatia-Trisidos* link is supported. The stomach of *T. semitorta* is similar to that of both *Anadara* and *Arca* and different from that of representatives of the Glycymerididae. It is, however, difficult, at first, looking only at the adult, to understand why *Trisidos* could not have evolved from a burrowing arcoid lineage, by posterior elongation, twisting and, in *T. tortuosa,* some degree of lateral flattening. There appears no reason for not deriving *Trisidos* from, say, an anadarine ancestor, especially as *T. semitorta* more closely fits the definition of the Anadarinae (Newell, 1969) than the Arcinae. However, the views of Newell (1969) and Tevesz & Carter (1979) are borne out by this research. Juvenile *T. semitorta* are byssally attached to the inside of empty bivalve shells; subsequently, attachment and the byssus are lost. The byssus functions in the classical manner as a means of securing post-larvae in a position suitable for the growth of the juvenile. Juvenile *T. tortuosa* and *T. semitorta* are not so twisted when young, twisting being a progressive condition.

The terms "torsion" and "twisted" require consideration. Traditionally *Trisidos* is referred to as the "twisted" ark, but McGhee (1978) replaced this with "torted." Generally, gastropods are torted, the mantle cavity moving from a posterior to an anterior position in larval development which is related to an "asymmetry in the development of the retractor muscles" (Garstang, 1929). In primitive prosobranchs (Crofts, 1955) and tectibranchs (Saunders & Poole, 1910), torsion is initiated by the contraction of a single asymmetrical, precociously developed larval cephalopedal retractor muscle. The term "twisted" has been
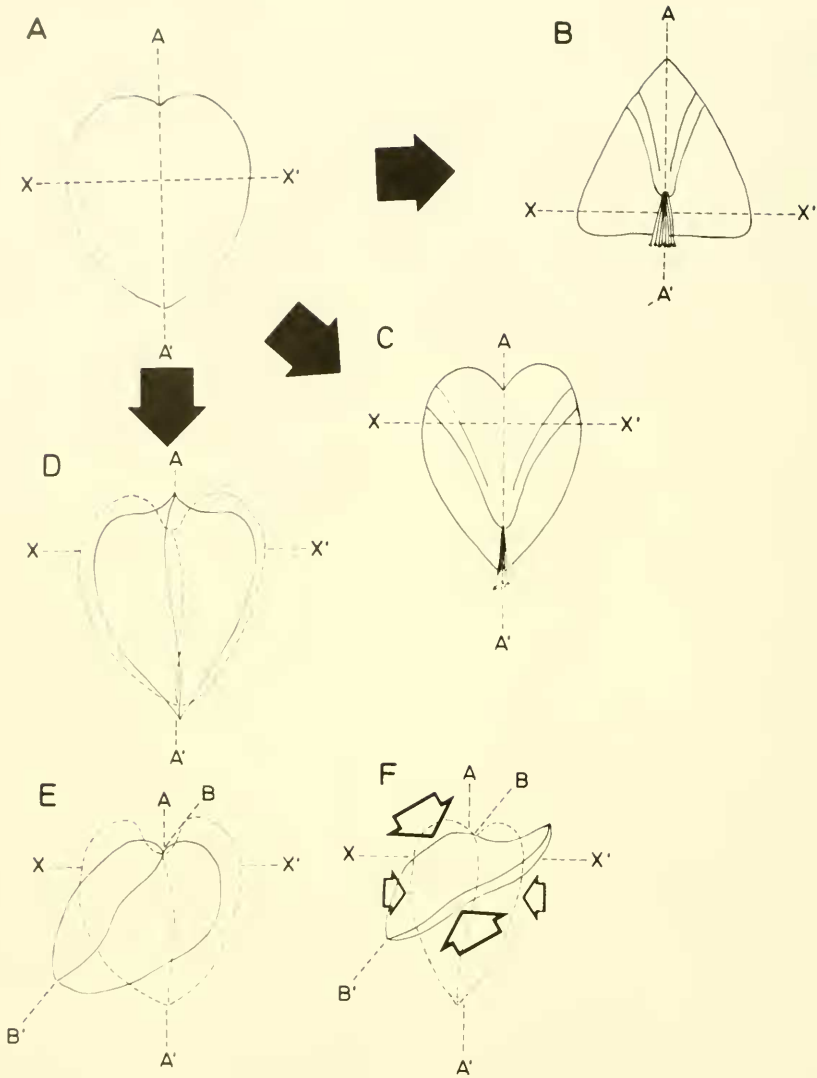
FIG. 22. A, Transverse section through the shell of an isomyarian, equilateral bivalve. B, Transverse section through the shell of a heteromyarian, equilateral bivalve, with byssus. C, Transverse section through an equilateral, partly heteromyarian, nestling bivalve. D, Transverse sections through the anterior (dotted lines) and posterior (solid lines) shell of a juvenile *T. semitorta*. E, The same through an adult *T. semitorta*. F, The same through an adult *T. tortuosa*. (Large open arrows indicate lateral compression in F). (A-A_1, the dorso-ventral axis of the shell; B-B_1, the dorso-ventral axis through the posterior region of the shell of *Trisidos*; X-X_1, the region of shell exhibiting the greatest shell width).

applied to *Trisidos* though, hitherto, it was not known how this was achieved. The process of twisting in *Trisidos* has obvious similarities and major differences with torsion of the larval gastropod. Thus, twisting results from the contraction of unequal, asymmetrically aligned posterior pedal retractor muscles. These can be regarded as "cephalopedal" re-

tractors because, though posteriorly located, they would in the primitive bivalve have withdrawn the head-foot. The difference is that twisting occurs *laterally* about the sagittal plane of the mantle shell and not by altering the mantle cavity from a posterior to an anterior position. Moreover, it would seem that twisting in *Trisidos* is a post-larval and not a

larval feature. It is contended that the term torsion should be used only with reference to that process characteristic of the larval gastropod. In *Trisidos* the term twisted should be used, as it more appropriately defines the situation and distinguishes a process that is interesting though of restricted phylogenetic importance.

From an isomyarian, infaunal, abyssate (except in the larva) ancestor (Fig. 22A), evolution in the byssally attached adult bivalves has proceeded in a number of directions. In the various heteromyarian bivalve lineages, e.g. Mytilacea and Dreissenacea (Yonge & Campbell, 1968) (Fig. 22B), the byssus acts as the point about which the reorganization of the body occurs. In epibyssate heteromyarian bivalves, the greatest shell width lies ventral to the mid-point of the dorsoventral axis of the shell. This ensures stability on wave-tossed, exposed beaches or in fast-flowing fresh waters (Morton, 1969). There are also heteromyarian byssally nestling species. In the nestling bivalve (Fig. 22C), the greatest shell width usually lies dorsal to the mid-point of the dorso-ventral axis of the shell. The narrow ventral region of the shell enables the shell to tightly fit into crevices. From Fig. 22D it can be seen that the juvenile *T. semitorta* is fundamentally a nestler, its shell form matching that of others (Fig. 22C). In the adult (Fig. 22E and F), the anterior end retains its typical nestling form. There is a morphological compromise which, perfectly suitable for neither juvenile nor adult, permits maintenance of both. Both forms are essential if juvenile and adult are to survive in fast-moving waters, but twisting optimises success for both. It should be noted that adult *T. semitorta* possesses no byssus and that the twisting process seen in the free adult is a continuation of a processs *begun* in the post-larva. The twisted shell allows *Trisidos* to lie in the sediment in a way that minimizes the effect of fast currents and scour. Tevesz & Carter (1979) suggested that in very twisted *T. yongei* lateral compression may reduce the ventilation efficiency of the mantle cavity. While this cannot be as acute in the more rounded *T. semitorta*, species of *Trisidos* occupy well-aerated sands, possibly facing into the current, so that the problems of ventilation are reduced. Even in *T. tortuosa,* the anterior region of the mantle cavity is still relatively unaffected by twisting and the mantle cavity functions in the usual manner.

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